

REVIEW

Reproduction by Fragmentation in Corals

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ABSTRACT: Production of new colonies by fragmentation of established colonies is shown to be an extremely important mode of reproduction and local distribution among major reef-building corals. This type of reproduction avoids the high mortality rates of larvae and juveniles and spreads the risk of mortality for the genotype. Fragmentation by corals with high growth rates results in their domination of certain reef zones, rapid growth of reefs on which these corals are abundant, and rapid recovery from disturbances. I conclude that a number of the most successful corals are adapted to fragment, i.e. have incorporated fragmentation into their life histories.

INTRODUCTION

Fragmentation of a single colony into 2 or more colonies appears to be the predominant mode of reproduction in certain corals and an important mode in others (Table 1). All of the coral species listed in Table 1 and discussed below are, ecologically and geologically, important members of their respective reef communities, with *Acropora cervicornis*, *A. palmata* and *Montastrea annularis* most often listed as the major reef-building corals in the Caribbean, *Pocillopora damicornis* the most important in the eastern Pacific,

and members of the Acroporidae and Poritidae of primary importance in the Indo-West Pacific**. These corals may all reproduce sexually as well as by fragmentation, but in general their local abundance and distribution on reefs appear to be due largely to the latter.

I define 'fragment' as a live portion of a coral colony that has become physically separated, due to the breakage of the skeleton, from the rest of the colony. The special case where the live surface of a coral becomes divided into 2 or more sections without breakage of the skeleton will be dealt with separately. Following Connell (1973), I consider a colony to be an individual; asexual reproduction in corals as used in this paper refers strictly to an increase in number of independent colonies rather than to growth of a single colony by budding new polyps. I treat colonies as individuals because they (1) recruit as individuals; (2) do not reproduce sexually until the colony has reached a certain size or age (Connell, 1973; Stimson, 1978); (3) often have characteristic growth forms for each species and in some cases even repair damage so as to restore the original colony shape (Stephenson and Stephenson, 1933; Loya, 1976a) suggesting integration of activities; (4) translocate materials within the colony (Pearse and Muscatine, 1971; Taylor, 1977); and (5) the ecologically relevant mortality rate is that for entire colonies.

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** Caribbean: Lewis (1960); Mesolella (1967); Glynn (1973); Goreau and Goreau (1973); Milliman (1973); Scatterday (1974); Adey (1975); Bak (1976, 1977); Macintyre and Glynn (1976); Shinn (1976); Bonem and Stanley (1977); Lighty (1977); Macintyre et al. (1977); Focke (1978); Gladfelter et al. (1978); Rogers (1979); Brown and Dunne (1980). Eastern Pacific: Squires (1959); Glynn et al. (1972); Porter (1972); Glynn and Macintyre (1977); Glynn et al. (1979). Indo-West Pacific: Wells (1954); Talbot (1965); Braithwaite (1971); Davies et al. (1971); Loya and Slobodkin (1971); Mergner (1971); Pichon (1971); Rosen (1971); Maragos (1972); Stoddart (1973); Dollar (1975); Chevalier (1977); Pichon (1977); Salvat et al. (1977); Scoffin (1977a, b); Ditlev (1978); Sheppard (1979, 1980a)

Table 1 Corals reported to reproduce by fragmentation

Species	Family	Growth form	Source
Caribbean			
<i>Acropora palmata</i>	Acroporidae	Branching	Bak and Engel (1979) Highsmith et al. (1980)
<i>Acropora cervicornis</i>	Acroporidae	Branching	Gilmore and Hall (1976) Shinn (1976) Tunncliffe (1978, 1980)
<i>Madracis mirabilis</i>	Pocilloporidae	Branching	Bak and Engel (1979)
<i>Porites furcata</i>	Poritidae	Branching	This paper
<i>Montastrea annularis</i>	Faviidae	Massive	Jones (1977)
Eastern Pacific			
<i>Pocillopora damicornis</i>	Pocilloporidae	Branching	Glynn (in press) Wellington (1981)
<i>Pavona clavus</i>	Agariciidae	Massive	This paper
Indo-West Pacific			
<i>Acropora aspera</i>	Acroporidae	Branching	Birkeland et al. (1979)
<i>Acropora acuminata</i>	Acroporidae	Branching	Randall (1973a)
<i>Acropora formosa</i>	Acroporidae	Branching	Grassle (1973) Sheppard (1981)
<i>Acropora hyacinthus</i>	Acroporidae	Branching	Grassle (1973) Sheppard (1981)
<i>Montipora</i> sp.	Acroporidae	Various	Grassle (1973)
<i>Porites compressa</i>	Poritidae	Branching	Maragos (1972) Dollar (1975)
<i>Porites lobata</i>	Poritidae	Massive	Dollar (1975)
<i>Porites lutea</i>	Poritidae	Massive	Highsmith (1980)
<i>Goniopora stokesi</i>	Poritidae	Massive	Rosen and Taylor (1969)
<i>All family members</i>	Fungiidae	Solitary	Wells (1966)

After considering a theoretical basis for the evolution of fragmentation, I summarize the growing evidence for the importance of this type of asexual reproduction in corals, relate life-history characteristics of fragmenting corals to predictions of the theory, and briefly discuss the ecological and geological consequences of coral reproduction by fragmentation.

THEORETICAL BASIS FOR THE EVOLUTION OF FRAGMENTATION

Possibly fragmentation is an inevitable consequence of being a relatively large, sessile organism, with a calcareous skeleton, and living in shallow marine environments; portions of colonies are simply broken off or separated from the rest of the colony by physical factors – such as currents or storms – and biological factors – such as predators or bioeroders. Alternatively, fragmentation in corals may be adaptive, i.e. selected for over evolutionary time and incorporated into the life history of many corals. I will attempt to demonstrate the validity of the latter hypothesis by comparing morphological features, habitat requirements, and life-

history characteristics of corals that commonly fragment and those that do not.

Definitions and Hypotheses

Morphology

If fragmentation is not adaptive, then breakage is an injury and corals should have evolved growth forms that reduce the probability of such damage. Thus, corals should tend to have compact growth forms with low profiles or small adult sizes (determinate growth), low-porosity (\approx high-strength) skeletons, and maintain live tissue over all parts of the skeleton to prevent invasion and weakening of the skeleton by boring organisms. Conversely, if fragmentation is adaptive, those corals in which it occurs should have a more diverse array of growth forms and should have evolved skeletal features such that fragmentation is likely to occur at some frequency related to the probability of survival of the fragments. In this case, corals should have large colonies with relatively high profiles and have skeletal strengths commensurate with growth form, characteristic wave or current stress encoun-

tered, and propensity to fragment. The combination of growth form, growth rate, and skeletal strength within a species should be such that fragmentation produces new colonies of a shape or size likely to survive. In this respect, regularly occurring structural weak points in the skeleton that increase the probability of breakage at those particular points, e.g. constrictions, regions of high porosity, systematic failure to maintain live tissue over (to prevent invasion by boring organisms) and enlarge skeletal zones likely to be mechanically stressed such as branch stems and column bases, or growth to the point of mechanical instability, will be considered as evidence that fragmentation has been selected for in a species.

The size and number of fragments produced by a coral colony are not independent and can be thought of as a continuum. Conceivably, corals could achieve a given level of asexual reproductive success by either producing many small fragments, each with a low probability of survival or a few large, highly viable fragments. Also, fragmenting corals should generally allocate little energy to maintaining live tissue over the entire skeleton for the purpose of excluding bioeroders since skeletal weak points may be inconsequential or even beneficial.

Habitats

If fragmentation is not adaptive, other factors being equal, then corals should occur in locations normally protected from strong currents and wave action in geographic locations seldom affected by storms, have life expectancies less than the average storm frequency, or reproduce at an early age. On the other hand, corals adapted to fragment, should have less restricted habitat requirements and life history features with respect to currents and storms. In fact, storms may indeed be major reproductive events for long-lived corals, provided they are not so severe as to kill the resulting fragments.

Life Histories

For organisms that have incorporated both sexual and asexual reproduction into their life histories, Williams (1975) listed several expected differences between offspring produced by each method (Table 2). For sessile, colonial organisms, he specifically proposed the Strawberry-Coral Model in which organisms reproduce vegetatively to form colonies that spread until their tolerance limits are met. Since these colonies are inevitably mortal, sexual reproduction serves for dispersal to other locations. Although Williams

Table 2. Expected differences between asexually and sexually produced offspring. Adapted from Williams (1975)

Asexual offspring	Sexual offspring
Large initial size	Small
Produced continuously	Seasonally limited
Develop close to parent	Widely dispersed
Develop immediately	Dormant
Develop directly to adult stage	Develop through a series of diverse embryos and larvae
Environment and optimum genotype predictable from those of parent	Environment and optimum genotype unpredictable
Low mortality rate	High mortality rate

considered growth of coral colonies by production of new polyps to be asexual reproduction, I will relate the predictions in Table 2 and the Strawberry-Coral model to life-history traits associated with reproduction by fragmentation as one test of the hypothesis that fragmentation has been acted upon by natural selection and become incorporated into the life histories of certain corals.

Within a species, success of asexual reproduction should enhance sexual reproductive success but not vice versa. High growth rates, for example, could be selected for because individuals that grow fastest produce the largest number of asexual offspring resulting in both greater sexual output per unit time* and longer life-span (see next paragraph) in which to reproduce. Conversely, those species that reproduce primarily sexually should develop features likely to further enhance sexual output such as reproducing at a younger age or producing more gametes at the expense of growth and maintenance (Harrigan, 1972), thus reducing the probability of fragmentation.

Mortality rates for clones, i.e. the original colony plus asexual offspring, should be considerably lower than for single colonies. If a colony is physically stressed, diseased (Antonius, 1977; Dustan, 1977), comes into contact with a superior competitor (Vicente, 1978), or is discovered by a predator (Endean, 1973; Glynn, 1976), the entire colony may be killed. If a colony has fragmented, however, the probability of mortality is independent for each fragment (to the same extent that it is for unrelated colonies of a species at a given

* Within a species, the larger the surface area, the greater the number of polyps in a colony and hence, the more gametes or larvae produced (Maragos, 1972). Over time, the surface area and number of polyps on 2 or more colonies should be greater than that of a single colony because of the restrictions imposed by colony shape, i.e. there is only space for a certain number of branches per colony, space competitors, available substratum, or proximity to the water surface

location). For example, using an annual mortality rate of 3 %, the joint probability of mortality for a parent plus 1 large fragment would be $(0.03)^2$, for a parent plus 2 large fragments $(0.03)^3$, and so forth*. Clearly, many combinations of fragment number and mortality rate are possible but the probability of genotype mortality must nearly always be less when there are 2 or more separate colonies, even if the probability of mortality per individual increases temporarily as a result of division of 1 large colony into several smaller colonies. Connell (1973) found mortality rates declined sharply with increasing colony size for very small colonies, but colonies with a surface area $\geq 81 \text{ cm}^2$ had an average mortality rate under 3 % per year. Consequently, continued growth of large colonies can reduce their mortality rate no more than 3 % (Fig. 1) and, in addition, breakage of large colonies may not result in any appreciable increase in mortality rate for them or their fragments if their size remains to the right of the inflection point on the mortality rate curve. These calculations lead to the prediction that species already having low mortality rates per colony would gain the most by fragmentation which, therefore, should be most common among long-lived species. For example, a colony with an annual probability of mortality of 0.10 would achieve a 10-fold reduction in the genotype mortality rate by producing 1 additional colony via fragmentation, but a coral with a probability of mortality of 0.05 would reduce the genotype mortality rate by a factor of 20. In addition, colonies derived from frag-

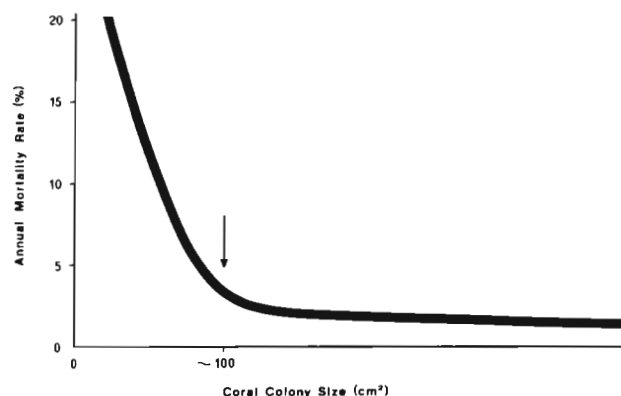


Fig. 1. Approximate annual mortality rate of corals as a function of colony size. Beyond the inflection point (arrow), there is little decrease in mortality rate with increasing coral colony size. Adapted from data of Connell (1973)

* Cook (1979), stressing the importance of vegetative reproduction in reducing the probability of mortality for plants, suggested that the 'extinction of the genotype becomes up to half as likely if two independent mortality events must occur'. However, the probability of genotype extinction should be the product of the probabilities of mortality for all independent members of the genotype

ments may subsequently produce fragments also, i.e. a geometric increase in colony number is possible. Theoretically, it appears that clones of fragmenting species have the potential to be virtually immortal, barring a catastrophic event (Harper, 1977) affecting the entire reef area on which all members of the clone occur.

Over evolutionary time, organisms capable of both reproductive modes should achieve a balance between sexual and asexual reproduction (Williams, 1975). Parthenogenetic organisms, for example, due to the great short-term advantage of asexual reproduction typically produce several asexual generations per each sexual generation. Usually, the different offspring types have different ecological roles, asexual produced during stable, predictable periods and sexual in response to unfavorable or less predictable conditions (Williams, 1975). Similarly, corals adapted to reproduce extensively by fragmentation should put more energy into growth and less energy into sexual reproduction per unit tissue biomass than corals less dependent on fragmentation or non-fragmenters. Here, the role of fragments should be to gain local distribution, colonize substrata (e.g. sand, space occupied by competitors) that larvae cannot, acquire space from competitors, and to spread the risk of mortality over several individuals. Because of the frequency of disturbances** or altered conditions affecting large reef areas (Scatterday, 1974; Antonius, 1977), sexual reproduction should be most advantageous in these corals as a mechanism for long distance dispersal, i.e. dispersal to other reefs (Williams, 1975; Jackson, 1979).

In addition to dispersal, Williams (1975) suggested that the sexual production of genetically diverse offspring would increase the probability of successful colonization of new locations. Further, Glesener and Tilman (1978) argued that sexuality is maintained in a community of interacting organisms by increasing the uncertainty of the direction and intensity of selection imposed by their interactions, i.e. the sexual production of genetically diverse offspring is an adaptation to the unpredictability of the genotypes of sexually pro-

** Most coral reefs are located in areas of frequent storm activity (Ball et al., 1967; Stoddart, 1971). An average of 4.5 hurricanes and 3.4 tropical storms occur in the Caribbean each year (Glynn et al., 1965). Hurricanes strike Belize reefs every 10 yr on the average (Stoddart, 1963); Ball et al. (1967) estimate that any particular Florida reef is affected by hurricanes once every 6 yr. In the Pacific, 70 cyclones of at least tropical storm strength (34–63 kt winds) passed within 180 nautical miles of Guam from 1948 to 1975 ($\bar{X} = 2.5 \text{ yr}^{-1}$) with significant typhoons ($> 64 \text{ kt winds}$) affecting Guam every 7 yr (Randall and Eldredge, 1977). Cyclones also occur frequently at New Caledonia and on the Great Barrier Reefs where 2 to 3 cyclones yr^{-1} affect some part of the Queensland coast (Brandon, 1973; Chevalier, 1973).

duced competitors and predators. These considerations are beyond the scope of the present paper although the relatively limited investment in sexual reproduction by several major reef-building corals (table 8) would seem not to support these hypotheses.

Thus, reduced allocation of energy to sexual reproduction among fragmenting corals and the occurrence of fragmentation among corals with low mortality rates per colony will be considered evidence favoring the hypothesis that fragmentation has been selected for in those corals.

EVIDENCE FOR REPRODUCTION BY FRAGMENTATION

Morphology and Habitats

Programmed Detachment

Asexual reproduction is highly developed in *Goniopora stokesi* (Poritidae) (Rosen and Taylor, 1969) and in the Fungiidae (Wells, 1966), both of which have adopted a free-living lifestyle. Fungiids are initially connected to the substratum by a short stem but eventually become detached, presumably by dissolution of or very limited production of skeletal material at the intersection of the polyp and stem. The stem, which remains attached to the substratum, may survive and generate more polyps in this manner (Wells, 1966). In addition, the detached polyps may produce new polyps on either their oral or aboral surface, which also break away and live free on the substratum. This double mode of asexual reproduction results in clumps of adults (clones) that all originated from a single planula larva (Wells, 1966).

In *Goniopora stokesi*, 'polyp balls' consisting of 1 to 30 polyps and a spherical, unattached skeleton are formed on the surface of adult colonies (Rosen and Taylor, 1969). Many 'polyp balls' can be produced at a time and may comprise 25 % of the surface area of the parent colony. When the 'polyp balls' reach a diameter of about 2 cm, they drop off and lie free on the surrounding sand. Rosen and Taylor (1969) concluded that, similar to the fungiids, this mode of asexual reproduction is an adaptation for colonizing sandy substrates. This conclusion is supported by Sheppard's (1981) work in the Chagos Islands. He found that *G. stokesi* 'polyp balls' colonized sand along lagoon reef margins, eventually resulting in extension of reef slopes.

Except that asexual reproduction does not occur, the Caribbean coral *Manicina areolata*, bears a number of resemblances to the Indo-Pacific fungiids (Goreau and Goreau, 1960). *Manicina areolata* is initially attached

to a hard substratum by a small, weak stem that is not enlarged as the coral grows. Eventually the colony breaks off and lives free on soft sediment areas around reefs. Both the fungiids and *M. areolata* tend to have rather flattened adult shapes with a large surface area relative to skeletal volume, can efficiently rid themselves of sediment, and can right themselves if overturned (Goreau and Goreau, 1960).

In all 3 of these examples, the corals are presumably released from the parent or stem when they have reached a size and shape likely to survive on a sandy substrate, an apparently suitable habitat for adults that cannot be colonized by larvae (Goreau and Goreau, 1960). *Goniopora stokesi* and the fungiids, due to asexual reproduction, are frequently found in extensive, monospecific clumps or patches (Wells, 1966; Rosen and Taylor, 1969; Sheppard, 1981). Also, the fungiids and *Manicina areolata* have determinate growth, so colonizing sand substrates may have the advantage of avoiding being overgrown or overtopped by reef-dwelling corals with indeterminate growth.

Caribbean Corals

The dominant shallow-water (≤ 6 m depth) coral on many Caribbean reefs, including exposed fringing and barrier reefs, is the elkhorn coral *Acropora palmata* (Fig. 2a), which often occurs in dense stands (Goreau, 1959; Storr, 1964; Scatterday, 1974). It was recently proposed that detachment of branches during periodic disturbances may be the primary mode of reproduction and distribution for this species (Highsmith et al., 1980). In Belize, 46 % of *A. palmata* branches and branch fragments broken off during Hurricane Greta, and which landed in sand-bottomed grooves, survived as did the original basal region of most colonies (Highsmith et al., 1980). Since there are typically several branches per colony*, and some branches broke into more than one piece, the total number of live elkhorn colonies on the reef apparently increased as a result of the storm. Survival of *A. palmata* fragments generated by storms has also been noted in Florida (Ball et al., 1967; Perkins and Enos, 1968) and Puerto Rico (Glynn et al., 1965); at Anegada, British Virgin Islands, many live colonies are detached from their original base (Dunne and Brown, 1979). At Jamaica, juvenile *A. palmata* are uncommon (Jackson, 1979) and at Curacao, only 2 of 252 juvenile corals in a series of 1-m² quadrats placed between 3 m and 9 m depth were *A. palmata* (Bak and Engel, 1979). Based on the lack of

* An average of 13 branches per colony (range 5–32, N = 65 colonies) occur on large *Acropora palmata* colonies in the San Blas Islands, Panama (unpubl. own obs.)

juveniles and the frequent observation of new colonies developing from fragments, Bak and Engel (1979) also suggested that *A. palmata* depends heavily on asexual propagation.

In the San Blas Islands, Panama, I recorded the proportion of *Acropora palmata* colonies derived from fragments (Fig. 2b). These data (Table 3) indicate that about two-thirds of the colonies originate asexually, in agreement with Bak and Engel's (1979) observations. Since hurricanes seldom affect Bonaire, Curacao, or the San Blas region, some combination of mechanical instability due to branch length, bioerosion (Hernandez-Avila et al., 1977), and minor storms, may be responsible for coral breakage in these locations. The number of fragments in reef grooves and sediment troughs, upside down colonies, and detached colonies of large size, suggest wave action is an important

source of coral breakage on San Blas reefs. Small storms, called Chocosanos, do occur in this region.

In addition, I examined the staghorn coral *Acropora cervicornis* (Fig. 2c) both in small clumps (Table 4) and at 1-m intervals along transects in large patches (Table 5) and recorded whether the colonies were attached, detached, or reattached. Approximately 40 % of the 2105 colonies were detached, 47 % reattached, and only 10 % to 16 % attached in their original location. Many colonies in the attached and reattached categories have very weak stems that break off at the slightest touch. The stems are seldom covered by live tissue and are consequently extensively infiltrated and weakened by burrowing sponges. Detached colonies, especially within large patches, are relatively stable under normal conditions because their branches are interwoven with those of other colonies. Many of the clumps occur in depressions and appear to originate by the transport of colonies from other locations. Clumps isolated on sand were not included in the study (Table 4) because all colonies in such clumps are detached or reattached to each other and would have consequently biased the data. *A. cervicornis* is most abundant (moderately exposed forereefs) at depths of 3 m to 10 m in my San Blas study sites, but is often the dominant coral at depths of 15 m to 20 m at other Caribbean locations (Goreau, 1959; Tunnicliffe, 1978, 1980; Highsmith et al., 1980).

At Jamaica where much of the forereef between –5 and –30 m is dominated by *Acropora cervicornis*, Tunnicliffe (1978, 1980) also found that over 80 % of the live colonies had been broken off at the base which was usually not covered by live tissue and thus infested with boring sponges. In addition, one or more branches had been broken off in over 60 % of the *A. cervicornis* colonies. The ubiquitous breakage and redistribution of fragments plus the almost complete absence of sexual recruits led Tunnicliffe (1978, 1980) to conclude that the great success of *A. cervicornis* was due to frequent fragmentation resulting in both repro-

Table 3. *Acropora palmata*. Number of colonies originating from asexual reproduction at several sites in the San Blas Islands, Panama. Colonies were examined as encountered while swimming parallel transects in zones of abundant *A. palmata* cover

Location	Percent asexual	Total No. colonies
Holandes Cays	69	321
Salada Salada	73	348
Marsagantupo	68	472
Midiatupo	62	483
Acuardargana	76	446
Total	$\bar{X} = 69$	2070

Although *Acropora palmata* fragments have characteristic shapes, it was sometimes impossible to determine the origin of colonies. When there was doubt as to a colony's origin, it was assigned to sexual reproduction. When it was not possible to see the base, it was not counted. Because of growth onto the substratum and production of new branches, older fragments become increasingly difficult to recognize

Table 4. *Acropora cervicornis*. Mean number of colonies in small clumps that were attached, detached, or reattached to the reef substratum. Both locations are in the San Blas Islands, Panama. Number of clumps in parentheses

Location		Per clump	No. of colonies		
			Attached	Detached	Reattached
Salar (39)	\bar{X}	17.2	1.7	7.6	7.9
	Range	2–65	0–8	0–23	0–40
	Percent		10	44	46
Achutupo (31)	\bar{X}	15.0	1.6	6.3	7.1
	Range	5–49	0–11	0–18	0–40
	Percent		11	42	47

Colonies were scored as attached if they were connected to the substratum and there was no evidence, such as a broken stem, that they had previously been attached elsewhere. Colonies were scored as detached if they were not connected to the substratum or to branches of other colonies and there was evidence that the colony had previously been attached elsewhere

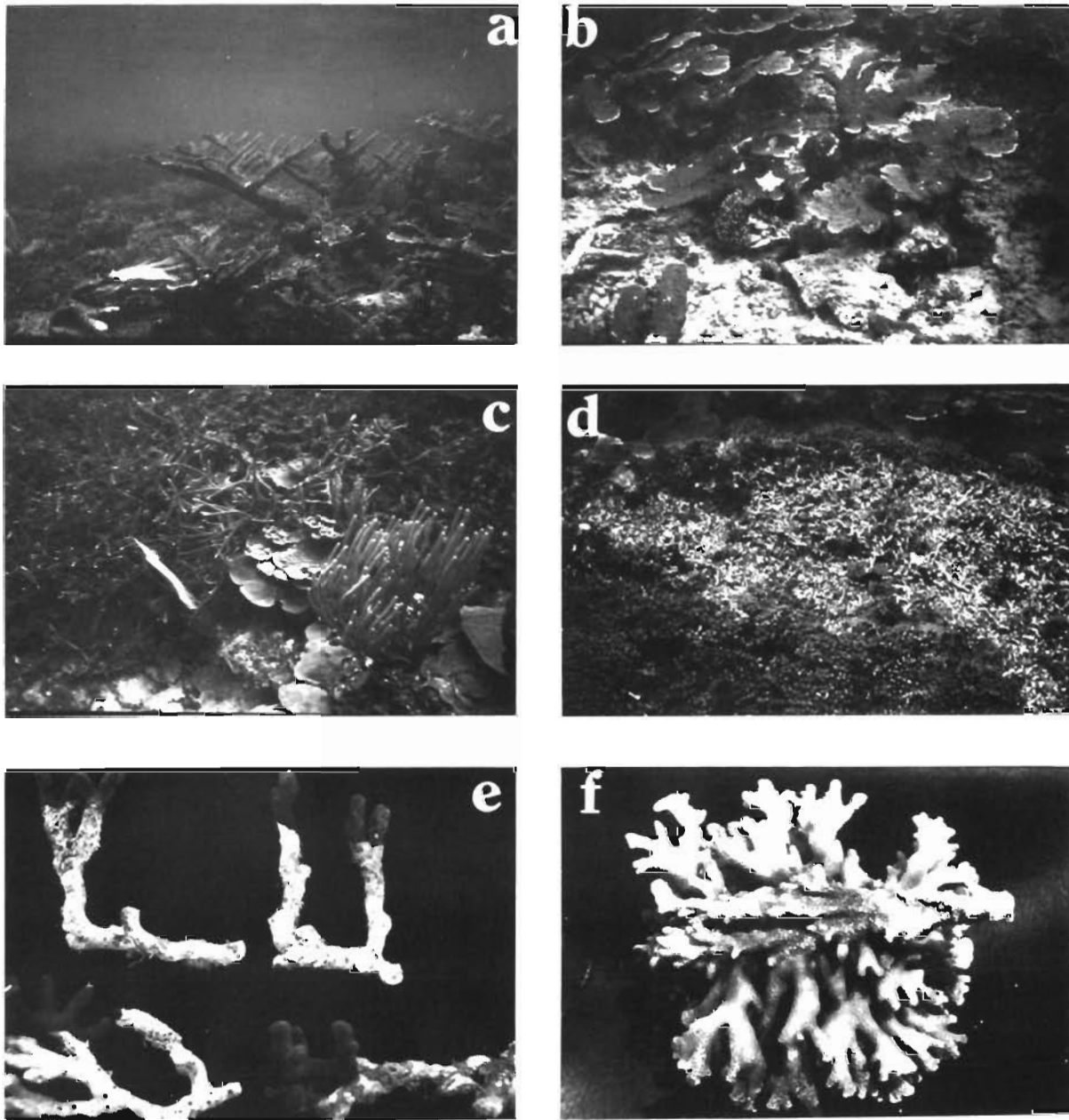


Fig. 2. (a) *Acropora palmata* at Bugatupo Reef, San Blas Islands, Panama. Note detached colony on left and branch stumps in center of picture. (b) *A. palmata* fragments at edge of dense stand. (c) Edge of *A. cervicornis* patch at Achutupo Reef, San Blas Islands, Panama. (d) *Porites furcata* patch with hole (light area) in patch possibly due to waves. Bugatupo Reef, San Blas Islands, Panama. (e) Detached *P. furcata* colony showing change in growth direction indicating colonies were previously attached with upward axis of growth from right to left. (f) Underside of a detached *Pocillopora damicornis* colony showing change in growth direction (into plane of photo). The colony was originally attached on the right end

duction and acquisition of space and that the fragile growth form (slender branches with high growth rate) of this coral has evolved to facilitate breakage.

Similarly, the majority of *Acropora cervicornis* colonies within the Florida Reef Tract apparently develop from broken branches of other colonies rather than from larval settlement (Gilmore and Hall, 1976). In fact, the rapid recovery of Florida reefs from hurricane

damage has been attributed to the survival and growth of numerous *A. cervicornis* fragments dispersed by the storms which increased the number of sites of active reef growth (Shinn, 1976; see also Perkins and Enos, 1968). Interestingly, no *A. cervicornis* larvae settled during an 8-month study of coral recruitment at Carysfort Reef, Florida (Dustan, 1977). *A. cervicornis* sexual recruitment was also quite rare at Jamaica during a 10-

mo study (Sammarco, 1980; see also Tunnicliffe, 1980). During a 1-year study of the distribution and abundance of juvenile corals at Curacao and a 1-month study at Bonaire, no juveniles of *A. cervicornis* were found although adults were present at the study sites and on other reefs in the region (Bak and Engel, 1979; Bak, pers. comm.). Also at Curacao and Bonaire, the delicately branched *Madracis mirabilis* appears to reproduce and spread primarily by breakage and survival of branches even though it usually occurs in more protected locations than the acroporans (Bak, 1976; Bak and Engel, 1979).

Another rather delicate branching coral in the Caribbean is *Porites furcata* which forms extensive patches at depths of 3 to 10 m on San Blas reefs (Fig. 2d). To evaluate the relationship of colony position within the patch to attachment to the substratum, three 25-m transects were placed over reef areas dominated by *P. furcata* at each of 3 islands (9 transects total). At each meter, colonies every 10 cm on either side of the transect out to 1 m (21 obs. per transect m) were examined to see if they were attached, detached, loose, or dead and their position in the patch, i.e. clump, edge, or hole, recorded. The occurrence of attached, detached, and loose colonies of live *P. furcata* is significantly affected by patch position (Table 6; $P \leq 0.001$, $X^2 > 400$ at each location, d.f. = 4). Colonies in the dead category were not included in the analysis because those in holes (Fig. 2d) were not actually *in situ* but were broken branches and stems apparently revealed by removal of overlying live colonies, presumably by wave action. Since only about 20 % of live *P. furcata* colonies are attached to the substratum, and then only weakly so due to the general occurrence of boring sponges in their stems (live tissue extends only a few cm below branch tips), it is not surprising that holes in the patches are common. These holes are recolonized by detached heads which are in all cases significantly more abundant at the edge of patches and in holes than expected by X^2 (Table 6). Examination of detached colonies usually reveals a 90° shift in the major growth

axis (Fig. 2e), indicating that the colonies originated in patches and toppled into holes. The redistribution of branching *Porites* colonies has also been reported at other Caribbean locations (Kissling, 1965; Connell, 1973; Glynn, 1973; Highsmith et al., 1980).

The predominant massive coral on most Caribbean reefs is *Montastrea annularis* which is broadly distributed with respect to both exposure and water depth (e.g. Goreau, 1959; Mesolella, 1967; Glynn, 1973; Milliman, 1973). Asexual reproduction can occur in 3 growth forms of this species: plates, columns, and hollow domes. Thin, overhanging skeletal plates, which are often produced around the edges of large colonies (Smith and Tyler, 1975; Jones, 1977), occasionally break off and colonize the adjacent substratum, resulting in lateral patch reef extension (Jones, 1977; Jones applied the term 'calving', in the sense that icebergs calve from glaciers, to fragmentation of colonies). Columnar growth forms are produced when the surface of a single, hemispheroidal colony becomes divided into several sections (Fig. 3d), eventually resulting in the upward growth of a number of columns, some of which may become detached due to bioerosion or storms (Lewis, 1960; Barnes, 1973; Scatterday, 1974, 1977; Jones, 1977). The large, dome-shaped colonies of *M. annularis* (Marszalek et al., 1977), hollowed out in large part by bioeroders (Storr, 1964), eventually collapse, breaking into several independent colonies (Smith and Tyler, 1975).

Eastern Pacific

The dominant reef-building coral in the tropical eastern Pacific is *Pocillopora damicornis*, a fast-growing coral with numerous branches (Glynn et al., 1972; Porter, 1972; Glynn and Macintyre, 1977; Glynn et al., 1979). Most *P. damicornis* reefs occur on the sheltered side of offshore islands but occasionally occur at more exposed sites (Glynn et al., 1972; Glynn and Macintyre, 1977). Along the edges of *P. damicornis* reefs,

Table 5. *Acropora cervicornis*. Number of attached, detached, or reattached colonies along and at 50 cm and 100 cm to either side (5 obs. at each m) of transects through large patches. See Table 4 for definitions of categories. All locations are in the San Blas Islands, Panama

Location	Transect length (m)	No. attached	No. detached	No. reattached
Salar	35	42	57	93
Achutupo	39	42	56	107
Ucubsui	56	32	99	163
Acuardargana	53	44	135	101
Total	183	160	347	464
Percent		16 %	36 %	48 %

Table 6. *Porites furcata*. Substrate attachment relative to position within or adjacent to dense patches of the coral. Clump: colony located within the patch surrounded by other *P. furcata*; edge: edge of patch; hole: hole within or adjacent to the patch (see Fig. 2d); other: corals of other species or coral debris; attached: connected to substratum; detached: not connected to substratum; loose: stem broken but supported in growth position by neighboring colonies. Values expected by X^2 test are shown in parentheses

Location	Transect length (m)	No. attached	No. detached	No. reattached
Salar	35	42	57	93
Achutupo	39	42	56	107
Ucubsui	56	32	99	163
Acuardargana	53	44	135	101
Total	183	160	347	464
Percent		16 %	36 %	48 %

clusters of branches commonly break free due to waves, bioerosion, or excavation by foraging fish and colonize the adjacent rubble/sand reef slope, resulting in lateral growth of the reef (Porter, 1972; Glynn, 1974, 1976, in press; Wellington, 1981). Transect data for 3 reefs in the Gulf of Chiriqui, Panama, clearly show that *P. damicornis* heads on the reef slope below the reef edge (Fig. 3a) are unattached and that a third or more of heads along the reef edge and in the reef itself are loose, i.e. clumps of branches detached from their stem but held in growth position by neighboring colonies (Fig. 4). These data combined with obvious changes in growth orientation of the detached clumps (Fig. 2f) strongly indicate that they originated from the reef. It should be noted, however, that *P. damicornis* fragments on reef slopes in the Gulf of Chiriqui probably have a higher mortality rate than colonies in the reef proper because the predatory seastar *Acanthaster planci* feeds preferentially on corals on the reef slope (P. W. Glynn, pers. comm.). *A. planci* does not occur on reefs in the Gulf of Panama.

Preliminary results from a recruitment experiment give an indication of the rate at which *Pocillopora damicornis* fragments colonize the reef slope. At Isla Uva, 5 study plots, each 30 m², along the reef edge were cleared of all living corals, including 173 *P. damicornis*. After 4.5 mo, a total of 25 *P. damicornis* colonies with a mean circumference of 42 cm (sd = 15 cm) had recruited and after 8 mo there were 38 live colonies (mean circ. = 38 cm, sd = 16 cm) present in the plots. Five colonies from the previous census were dead or missing. After twelve months, 66 colonies (mean circ. = 38 cm, sd = 12 cm) were found in the plots. Only 18 of these heads were present at the 8-mo point. A storm that occurred between the last two censuses resulted in the breakage and movement of many corals at Uva (A. Velarde, pers. comm.), probably accounting for this high turnover rate. The size of the new colonies clearly indicates they were fragments. If recruitment continues at this rate ($Y = 5.35x - 0.5$, r^2

= 0.98; where Y = number of colonies; x = number of months), the original number of colonies will be restored in the study areas in less than 3 yr.

The dome-shaped colonies of another eastern Pacific coral, *Pavona clavus*, like the *Montastrea* colonies mentioned above, are weakened by burrowing organisms, especially *Lithophaga* spp. (Table 7), resulting in collapse and breakage of the domes into several colonies (unpubl. obs.).

Indo-West Pacific

In Guam, most colonies of the staghorn coral *Acropora aspera* are derived from fragments, 79 % of colonies living unattached and the remainder, though attached, apparently originating from fragments (Birkeland et al., 1979; see also Randall and Eldredge, 1977). Fragmentation, combined with regeneration and fast growth rates, account for the dominance of *A. aspera* and *A. acuminata* in the Inner Reef Flat Sub-zone (350 to 380 m wide) at Guam (Randall, 1973a). Reports of *Acropora* spp. fragments founding new colonies also come from Australia (Stephenson et al., 1958; Connell, 1973), Enewetak (Stimson, 1978), Chagos (Sheppard, 1981) and the Red Sea (Mergner, 1971). In the latter case, *Acropora* fragments from the upper reef slope gave rise to an entire reef zone (Secondary *Acropora* Zone) on the lower slope.

Among the Poritidae, *Porites compressa* – probably the most important reef-building coral in Hawaii (Maragos, 1972; Dollar, 1975; Stimson, 1978) – forms thickets which expand by growth of individual colonies and by survival and growth of broken branches around the periphery of the thicket. Thickets may also be initiated in new locations by the survival of branches dislodged and scattered about by waves (Maragos, 1972; Dollar, 1975). Other branching poritids may reproduce in this manner also (Connell,

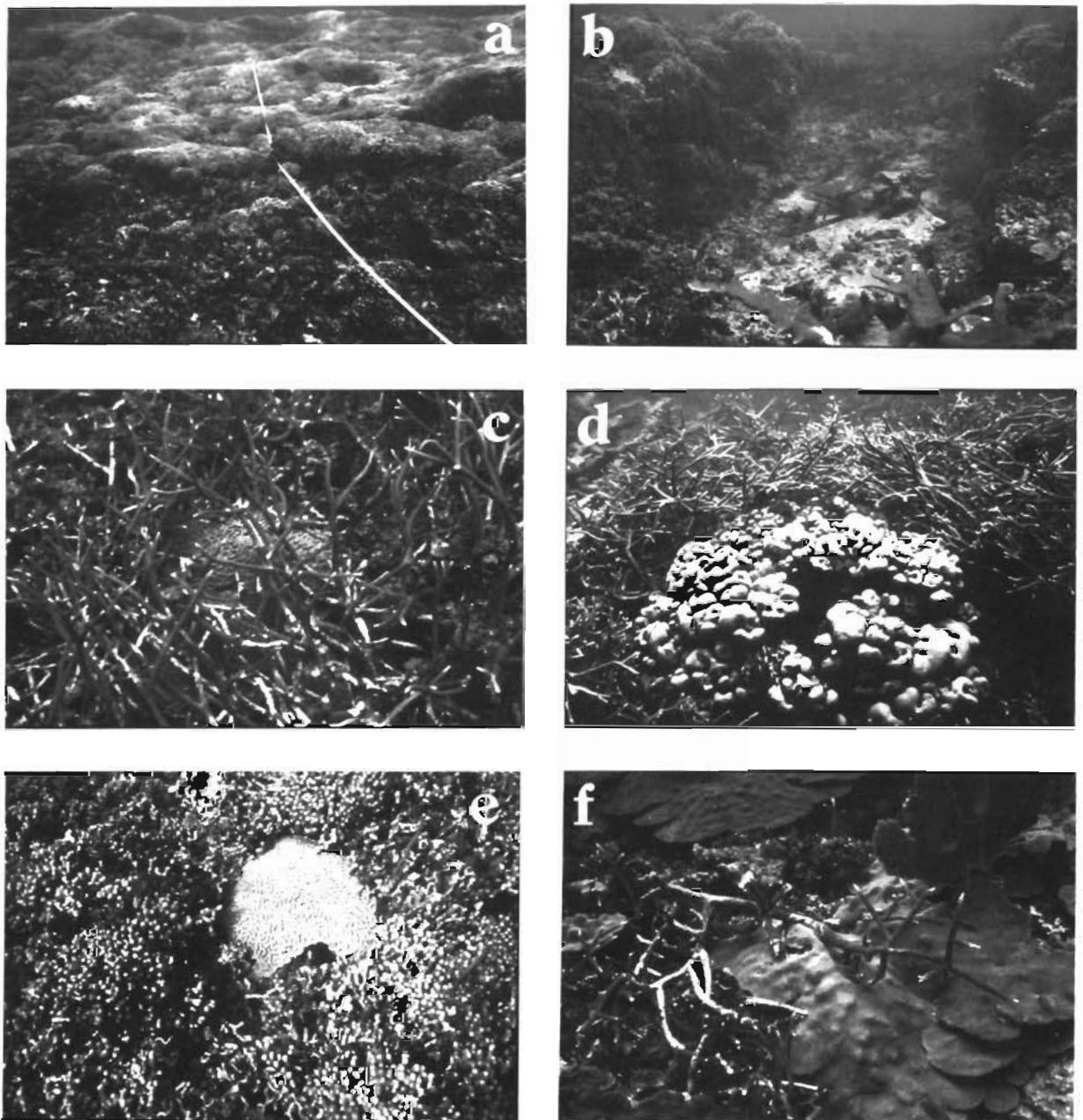
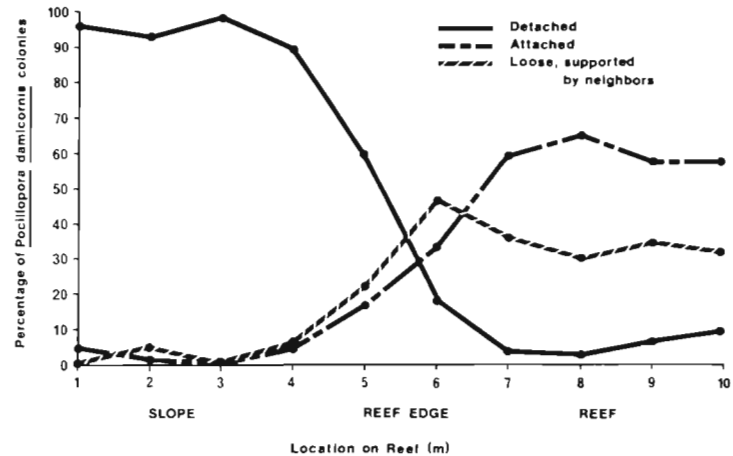


Fig. 3. (a) Transect site on *Pocillopora damicornis* reef, Isla Uva, Gulf of Chiriqui. Note detached corals below reef edge, foreground; see Fig. 4. (b) Groove between 2 coral spurs, Salar Reef, San Blas Islands, Panama. Note *Acropora palmata* fragments in groove; far end is dammed. (c) Massive head of *Diploria* being overtopped by the staghorn coral *A. cervicornis*. (d) Massive head of *Montastrea annularis* being overtopped by *A. cervicornis*. Branches of the latter species grow approximately 10–15 cm yr^{-1} . (e) Massive colony of *Diploria* in process of being overtopped by *Porites furcata*. (f) Massive head of *M. annularis* on which a fragment of *A. cervicornis* has fallen. The latter has been killed at places where the 2 corals are in contact but the massive coral is in danger of being shaded out by future growth of the live parts of the staghorn coral

1973; Randall and Eldredge, 1977). At many Indo-Pacific locations, the massive coral *Porites lutea* forms microatolls on intertidal reef flats (Dana, 1853; Scoffin and Stoddart, 1978; Highsmith, 1980a, 1981). Low tides prevent upward growth of microatolls so live tissue is restricted to the periphery of the colonies resulting in a

flat, more or less circular shape. At Eniwetok, microatolls detached from the reef due to their relatively small basal attachment and the activity of boring organisms, are transported by currents across the smooth reef flat to the edge of the lagoon where their growth is less restricted by low tides (Highsmith,

Fig. 4. *Pocillopora damicornis*. Percentage of attached, detached, and loose heads along 9-m transects at 3 reefs in the Gulf of Chiriqui, Panama (Isla Uva, 10 transects; Isla Secas, 10 transects; unnamed island, 7 transects). Observations were made on 5 colonies at each m mark on the transect, 1 under the transect line and 2 on either side of the line at distances of 50 cm and 100 cm. The transect was placed with the reef edge near the center. Total no. of observations = 1350



1980a). Frequently, parts of the microatoll margin which have encrusted onto the reef flat, break off the colony when it is dislodged and remain attached to the reef at the original site. Up to a dozen separate colonies, marking the outline of the original colony, may result from the detachment of a single microatoll (Highsmith, 1980a). For the closely related *P. lobata* in Hawaii, Dollar (1975) reported fragments were broken from colonies during a winter storm and transported several meters down the reef slope. The overall movement of living coral fragments and detached colonies resulted in a shift of peak percentage live cover 10–15 m further offshore and 5–10 m deeper.

Division of Colonies by Partial Mortality

Another mechanism of separation of single colonies into several partially independent units involves death of the intervening tissue between various portions of the colony growth surface (Lewis, 1960, 1974; Barnes, 1973; Connell, 1973; Scatterday, 1974, 1977). Thus, the

Table 7. Mean number of *Lithophaga* spp. (primarily *L. aristata* and *L. plumula*) burrows per 100 cm² in the underside of *Pavona clavus* hollow domes. Live: burrows still occupied by the bivalve. Dead: burrows broken open, probably by the triggerfish *Pseudobalistes naufragium*, and bivalves removed. Parentheses: no. of quadrats

Head	Mean no. <i>Lithophaga</i> spp./100 cm ²		
	Live	Dead	Total
A (5)	16.2	7.8	24.0
B (6)	5.2	16.7	21.9
C (4)	7.5	14.8	22.3
D (4)	11.8	13.0	24.8
E (4)	6.5	23.3	29.8
F (2)	11.5	5.0	16.5

coral tissue is divided into several sections but the skeleton is not fractured, at least initially (skeletal surfaces not covered by live tissue are likely to be invaded by boring organisms, increasing the probability of skeletal fracture; Tunnicliffe, 1978; 1980; Highsmith, 1981). This type of colony separation occurs in the Caribbean corals *Montastrea annularis* (Lewis, 1960, 1974; Scatterday, 1974, 1977; Hughes and Jackson, 1980; see Fig. 3d), *Porites astreoides* (Lewis, 1974; Bak, 1976), *Agaricia agaricites* (Lewis, 1974; Bak, 1976; Hughes and Jackson, 1980), *A. lamarcki* (Hughes and Jackson, 1980), *Helioseris cucullata* (Hughes and Jackson, 1980), and *Meandrina meandrites* (Bak, 1976) and in the eastern Pacific coral *Pavona clavus* (Glynn et al., 1972; their Fig. 7). In a 90 m² study area on the reef slope at Heron Island, Australia, one or possibly 2 colonies of each of 2 species of *Montipora* had separated into over 100 colonies and, similarly, 1 or 2 *Acropora formosa* had split into 77 colonies and 1 or 2 *A. hyacinthus* into 45 colonies (Grassle, 1973; see also Sheppard, 1980a). Branching *Porites* colonies also separate in this manner at Heron Island (Connell, 1973).

This type of colony separation may not result in as complete independence of mortality for the resultant individuals as fragmentation, depending upon the major sources of mortality, and does not provide the opportunity for increased local distribution and acquisition of space although skeletal weak points resulting from these dead zones may contribute to eventual fragmentation.

Summary

Morphologies of fragmenting species essentially span the entire range of coral growth forms from small, delicately branched to large, massive colonies. While some of these corals occur in protected habitats, nearly

all of them also occur in exposed sites and some are even confined to or at least are most abundant on forereefs. Certainly, all occur at locations affected by storms. Thus, the variety of growth forms, type of habitats occupied and geographical range of the corals discussed above are in contrast to those expected if fragmentation were generally maladaptive.

Life History Characteristics

Data on life history features are limited to just a few of the several hundred hermatypic coral species but the available evidence (Table 8) generally supports the theoretical predictions made earlier. Non-fragmenting coral species tend to (1) release planulae throughout most of the year, (2) release more planulae per colony than corals of a similar size in the fragmenting group, (3) become sexually mature at an early age (≈ 2 yr), (4) have many juveniles present on reefs, (5) grow slowly or at least more slowly as they become older, (6) have determinate growth resulting in relatively small adult colony sizes, (7) have a relatively short life expectancy, and (8) are poor space competitors (Maragos, 1972; Connell, 1976; Bak and Engel, 1979).

Life history characteristics associated with fragmenting species (Table 8) are generally the opposite of those for non-fragmenting corals. Fragmenting species (1) may release gametes rather than brood larvae, or else (2) produce fewer larvae per colony, (3) may only be ripe for a few months each year, (4) may not become sexually mature until 8–10 years old, (5) populations are dominated by adults with juvenile colonies being rare, (6) have high growth rates, (7) have indeterminate growth and become quite large, (8) are long-lived, and (9) are, except for *Porites lutea*, moderate to very good space competitors (Maragos, 1972; Connell, 1976; Shinn, 1976; Bak and Engel, 1979; Sheppard, 1979).

The Fungiidae, to the extent generalizations can be made from data on only a few members of this family, have characteristics of both groups. Release of planula larvae has actually only been observed in one species but in that case several hundred were released daily for several days each month for 8 mo of the year (Wells, 1966). Conversely, no larvae were found during a nine-month study of *Fungia scutaria* at Hawaii, although young heads, produced by budding, were common (Harrigan, 1972). I have listed this family as having small adult sizes but some species become rather large, one reaching up to 1 m in length (Wells, 1966). It would be interesting to know whether or not various fungiids emphasize one or the other mode of reproduction and, if so, the life history characteristics associated with each.

In a study of 7 Hawaiian and 12 Enewetak coral

species, Stimson (1978) only observed release of larvae in corals (2 Hawaiian and 7 Enewetak species) characteristically found on reef flats or in shallow water. He suggested that reef flat or shallow water species were 'weedy' as indicated by production of numerous larvae, beginning at a comparatively early age (≈ 2 yr), during all or most of the year. In contrast, 5 Hawaiian coral species characteristic of deeper water or with broad depth distribution, which did not release larvae, were examined histologically each month and eggs were found in 4 of the species but only 1 contained eggs more than 2–3 mo of the year. Stimson (1978) also found two shallow-water acroporans that did not release planulae and suggested they may reproduce by survival of branches broken off during storms. It has since been reported that one of them, *A. aspera*, reproduces almost entirely by fragmentation in Guam (Birkeland et al., 1979).

In addition to Stimson's (1978) observations, Duerden (1902) reported that *Acropora* and *Montastrea* (= *Orbicella*) species in Jamaica as a rule did not contain sexual cells and Marshall and Stephenson (1933) only observed release of planulae in two of ten Great Barrier Reef corals.

Possibly corals reproducing by fragmentation, rather than brood larvae, limit their expenditure on sexual reproduction to the release of sperm and eggs during a relatively short period of the year and perhaps not even annually (Connell, 1973). In this respect, fragmenting coral species resemble a number of fresh-water invertebrates that typically reproduce asexually as long as conditions are favorable and sexually only in anticipation of unfavorable conditions, such as winter. However, sexual phases may be infrequent or even absent in large lakes (Williams, 1975; Maynard Smith, 1978) where, similarly to tropical marine habitats, environmental conditions are relatively stable.

With regard to Stimson's (1978) finding that reef flat species tend to reproduce sexually, perhaps coral fragments are too unstable to colonize effectively certain habitats such as surf zones or wave-swept reef flats. Very steep or vertical walls may be another reef location neither readily colonized by fragments nor dominated by a fragmenting species and thus occupied by species emphasizing sexual reproduction or by a highly diverse assemblage of species reflecting chance larval settlement. Severely disturbed areas, i.e. where fragments have been killed or transported elsewhere, on reefs are also likely to be colonized initially by competitively subordinate species producing large numbers of sexual propagules (Mayor, 1918; Grigg and Maragos, 1974; Stoddart, 1974; Connell, 1978; Bak and Luckhurst, 1980).

There are many ecological explanations for the evolution of high growth rates in corals, e.g. escaping

Table 8. Comparison of life history characteristics for corals whose abundance and distribution on reefs is due primarily to sexual reproduction or primarily to asexual reproduction. Dash: no information available

Characteristics, Species	Release larvae ^a	Juveniles abundant	Growth rate ^b	Adult size	Life expectancy ^c	Sources ^d
Sexual reproduction dominant						
<i>Agaricia agaricites</i>	Yes	Yes	—	small	short	1, 2, 3
<i>Cyphastrea ocellina</i>	Yes	—	low	small	short	4, 5, 6, 7, 8
<i>Pocillopora damicornis</i> ^e	Yes	Yes	low	small	short	5, 6, 7, 8
<i>Stylophora pistillata</i>	Yes	Yes	low	small	short	9
Asexual reproduction dominant						
<i>Acropora aspera</i>	No	No	high	—	—	8, 10
<i>Acropora cervicornis</i>	No	No	high	large	long	11, 12, 13, 14, 15, 16, 17
<i>Acropora palmata</i>	No	No	high	large	long	3, 11, 14, 16, 18, 19
<i>Porites compressa</i>	No	—	high	large	long	5, 6, 7, 8
<i>Porites lutea</i> ^e	No	No	high	large	long	20, 21, 22
<i>Pocillopora damicornis</i> ^e	No	No	high	large	long	23, 24, 25, 26, 32
<i>Madracis mirabilis</i>	—	No	high	large	—	2, 27, 28
<i>Montastrea annularis</i>	No	No	high	large	long	2, 3, 11, 14, 29, 30
Fungiidae	see text	—	f	small	—	5, 6, 31

(a) Observed to release larvae. Some corals not observed to brood larvae will, with further study, probably be found to do so

(b) Linear rate of branch extension or radial growth in massive corals. Low and high are relative to other species occurring in the same region and having a similar growth form. Rates are for long-term growth so species with high initial growth rates that soon decline (determinate growth) are considered to have a low growth rate

(c) For adult colonies

(d) 1: Dustan (1977); 2: Bak and Engel (1979); 3: Bak and Luckhurst (1980); 4: Edmondson (1929); 5: Harrigan (1972); 6: Maragos (1972); 7: Stimson (1976); 8: Stimson (1978); 9: Fishelson (1973); Loya (1976 b, c); Rinkevich and Loya (1979 a, b); 10: Birkeland et al. (1979); 11: Duerden (1902); 12: Gilmore and Hall (1976); 13: Shinn (1976); 14: Gladfelter et al. (1978); 15: Tunnicliffe (1978, 1980); 16: Sammarco (1980); 17: R. Bak (pers. comm.); 18: Jackson (1979); 19: Highsmith et al. (1980); 20: Highsmith (1979); 21: Highsmith (1981); 22: J. Stimson (pers. comm.); 23: Birkeland (1977); 24: Glynn (1977); 25: Glynn and Macintyre (1977); 26: Glynn (in press); 27: Bak (1976); 28: Bonem and Stanley (1977); 29: Smith and Tyler (1975); 30: Jones (1977); 31: Wells (1966); 32: Wellington (1981)

(e) *Pocillopora damicornis* has remarkably different life-history features in Hawaii and Panama (ref's in Table). In Panama, it is the major reef builder, is the competitive dominant, has a high growth rate ($\approx 3\text{--}4\text{ cm-yr}$; Glynn, 1977), has indeterminate growth, and recruitment of sexual propagules is rare (Wellington, 1981; Glynn, in press). In Hawaii, *P. damicornis* is apparently a fugitive species, is competitively subordinate, has a low growth rate ($\approx 1.4\text{ cm-yr}$; Edmondson, 1929) and small adult size, and is noted for production of planula larvae. These populations are probably genetically isolated but the origin of *P. damicornis* in the Eastern Pacific is controversial. It occurs in Miocene and Pliocene Fossil deposits (Durham, 1966) but Panamanian *P. damicornis* reefs are only $\approx 6000\text{ yr}$ old (Glynn and Macintyre, 1977; Glynn, in press). For a discussion of long-distance dispersal versus vicariance with regard to eastern Pacific corals, see Heck and McCoy (1978). Stimson (1978) noted *P. meandrina* reproduces very differently at Enewetak and Hawaii. Also, *Porites haddoni* (= *P. lutea*?) at Low Isles, Australia released large numbers of planulae from January through June (Marshall and Stephenson, 1933) but planulation has not been observed in *P. lutea* at Enewetak (J. S. Stimson, pers. comm.)

(f) Growth rates of Fungiidae are reported to be high by some workers (e.g. Ma, 1957) and low by others (e.g. Maragos, 1972). The latter found that growth in *Fungia scutaria* slowed with increasing size

the high mortality rates for small colonies or growing fast enough to shade-out competitors (Connell, 1973). High growth rates often result in large colonies which are the most susceptible to breakage due to mechanical instability, large surface area presented to currents, or weight. Thus, fragmentation may have originated as an inevitable consequence of selection for high growth rates. Whether corals have subsequently evolved any specific adaptations such as particular growth forms or skeletal features resulting in fragments of a size or shape most likely to survive as, for example, in the Fungiidae or *Goniopora stokesi*, is in need of investigation.

The relationship between the size and possible number of fragments produced by a colony is indicated in Fig. 5. It appears that most fragmenting species are near the large-fragment end of the continuum. The low survivorship of small fragments during storms (Highsmith et al., 1980) and high mortality rates for small colonies (Connell, 1973; Loya, 1976b, c; Schuhmacher, 1977; Hughes and Jackson, 1980) probably make asexual reproduction via numerous small fragments a less likely course of coral evolution. Some point must be reached toward the left end of the continuum (Fig. 5) where a coral is more successful by investing energy in production of large numbers of sexual propagules

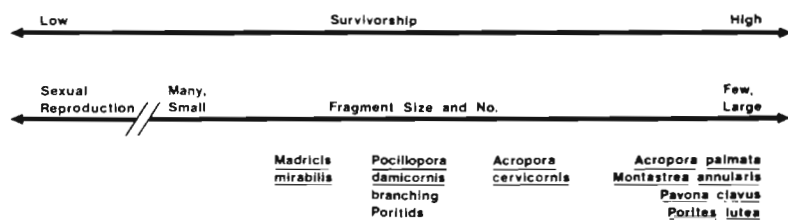


Fig. 5. Proposed relationship between coral fragment size and survivorship. A few examples are given, ranked according to typical fragment size. See text

rather than in growth of comparatively few fragments. The corals with relatively small fragments tend to occur in somewhat more protected habitats than those corals on the right end of the continuum. For a given level of survivorship, fragments should be larger in habitats where the sediment is less stable, i.e. where water energy is high, than in habitats where the sediment is more stable and, in both cases, fragments lacking efficient cleansing and righting behaviors should be larger than the fragments produced by corals with programmed detachment.

Fragment shapes most conducive to survival would seem to be those well developed in 3 dimensions, e.g. *Acropora cervicornis* in which branches tend to produce 2 or 3 new branches at 1-yr growth intervals (≈ 12 cm) (Shinn, 1976; Tunnicliffe, 1978, 1980), so that regardless of how they come to rest, some part of the fragment will be off the substratum and, hence, less likely to be buried or scoured. Tunnicliffe (1978, 1980) found that *A. cervicornis* fragments with multiple branches were more likely to survive than unbranched fragments. Both *A. cervicornis* and *A. palmata* have dense, heavy skeletons (Highsmith, 1981) which may prevent multiple breakage of fragments into very small fragments and also reduce transport of the fragments, because of their weight, to less favorable reef zones (Tunnicliffe, 1978, 1980; Highsmith et al., 1980). Clearly, the potential for fragmenting is much greater in branching corals because branches grow rapidly, are produced in large numbers, and are readily broken by biological and physical disturbances. It has even been suggested that some species grow continuously and that branches not otherwise detached ultimately break of their own weight (Maragos, 1972; Bak, 1976).

With respect to Williams' predictions (Table 2), the characteristics of coral asexual offspring meet them rather well. Fragments are large relative to coral larvae or juveniles and production is continuous in that fragments are produced by colony growth, although actual fracture of the colony may be periodic. Fragments, by virtue of their large size, tend to remain near the parent where the environment is more predictable and the mortality rate is consequently lower. The fragments represent an instantaneous adult although how soon fragments actually reproduce sexually may depend upon their size and extent of breakage-related damage.

The characteristics of sexual offspring of corals, with the exception of dormancy (larvae may, however, delay settlement in the absence of appropriate cues; Harrigan, 1972; Rinkevich and Loya, 1979a), generally meet Williams' (1975) predictions also. Larvae, as well as juveniles, are small and are produced seasonally or periodically in at least some cases (Duerden, 1902; Wells, 1966; Loya, 1976; Stimson, 1978). Larvae may be planktonic for as little as 2 d or as long as several wk and presumably are widely dispersed relative to fragments (Harrigan, 1972; Connell, 1973; Rinkevich and Loya, 1979a). Larval mortality rates are unknown but are probably very high (Connell, 1973; Loya, 1976b, c). Coral reefs are relatively small, isolated structures in the oceans with the majority of their surface area composed of sand or other soft sediments (Cloud, 1959; Goreau, 1959; Storr, 1964; Mergner and Scheer, 1974; Purdy, 1974; James et al., 1976; Orme, 1977; Highsmith et al., 1980) which are unsuitable for larval settlement (Marion, 1883; Vaughn, 1909; Stephenson, 1931; Hada, 1932; Motoda, 1939), and having a large proportion of the hard substratum already occupied, particularly by potential predators and space competitors (e.g. corals, soft corals, gorgonians, sea anemones, hydroids, algae) (Harrigan, 1972; Schuhmacher, 1974; Benayahu and Loya, 1977; Birkeland, 1977; Jones, 1977; Birkeland et al., 1979; Rinkevich and Loya, 1979b; Highsmith, 1980b). Also, Storr (1964) reported the periodic occurrence of heavy siltation sufficient to smother small, juvenile corals. Thus, settlement sites are not only isolated and far apart but many of the otherwise most favorable sites on reefs are unstable, unavailable, or unsafe.

Mortality rates for juvenile coral colonies, like those for larvae, are not well documented but appear to be very high also (Connell, 1973; Loya, 1976b, c; Schuhmacher, 1977; Bak and Engel, 1979). For example, Harrigan (1972) found that when *Pocillopora damicornis* larvae settled on pieces of dead, algal-coated coral, the new juveniles were killed during the night by small crustacean and annelid predators. Similarly, Maragos (1972) found only 2 of 60 newly settled *P. damicornis* alive after a period of just 2 mo. Bak and Engel (1979) monitored 390 juvenile corals of various species for a period of 6 mo during which one-third died and one-third was damaged or prevented from growing by competitors or sedimentation. These may

also be the major sources of mortality for small corals in Jamaica (Hughes and Jackson, 1980). During 2 consecutive 3.4 yr study periods, Connell (1973) found a clear relationship between colony size and mortality. For corals with surface areas of 1 to 40 cm², 41 to 80 cm², and ≥ 81 cm², the percentage mortality per period was approximately 50 %, 28 %, and 9 %, respectively. Thus, coral mortality rates appear to be strongly size dependent.

Conclusions

In view of the evidence presented above on the morphologies, habitats, and life histories of fragmenting corals, I conclude that reproduction by fragmentation occurs on a number of levels ranging from a rare or occasional event to a central feature in a coral's life, and that corals reproducing extensively by colony fragmentation have all the characteristics expected to have evolved in organisms that reproduce both sexually and by more traditional forms of asexual reproduction such as budding, runners, or parthenogenesis, i.e. several major reef-building corals have incorporated fragmentation into their life histories.

ECOLOGICAL AND GEOMORPHOLOGICAL CONSEQUENCES

Detached coral fragments usually move downslope or downstream (Mergner, 1971; Jones, 1977; Highsmith, 1980a). *Acropora palmata* and *Porites lutea* provide good examples. At Eniwetok, *P. lutea* microatolls on reef flats are prevented from growing upward more than a few cm by emersion at low tide. Detached microatolls are moved downstream to the edge of the lagoon where the water is deeper, permitting additional growth and resulting in lagoonward extension of the reef. The pieces of microatoll remaining encrusted to the reef grow into new microatolls (Highsmith, 1980a). At Belize, *A. palmata* occurs in the shallow spur and groove zone of the reef where continued growth may be limited by the proximity of branch tips to the water surface or crowding. Branches broken off during storms fall into the sand-bottomed grooves where about one half survive. These branches initiate new colonies and the original colony regenerates branches (Highsmith et al., 1980).

On many reefs in the San Blas Islands, fragments of *Acropora palmata*, *A. cervicornis*, and *Porites furcata* have colonized the grooves in the spur and groove zone so successfully as to fill or dam them (Fig. 3b).

In the above examples, fragments colonize sand bottoms, an extensive habitat on reefs that cannot be

colonized by larvae. Other corals reported to colonize soft bottoms in this manner are *Acropora acuminata* (Randall, 1973a), *Porites cocosensis* (Randall and Eldredge, 1977), *P. compressa* (Maragos, 1972), *P. lobata* (Dollar, 1975), *Montastrea annularis* (Jones, 1977), *Goniopora stokesi* (Rosen and Taylor, 1969; Sheppard, 1981), and the Fungiidae (Wells, 1966). Fragmentation and/or movement of fragments also results in (1) reef extension, (2) initiation of patch reef formation, (3) development of monospecific coral thickets in major reef zones, and (4) possibly avoidance of reef-bound competitors and predators.*

The development of coral thickets, i.e. monospecific stands covering large areas on reefs (e.g. Fig. 3a) is of considerable importance. Thickets expand by the rapid growth of branches around the periphery. Many break and fall onto the surrounding substrate, covering or shading competitors and providing hard substrate for growth of other branches, or producing new branches of their own if they survive. This cascading of branches is a superior competitive mechanism resulting in the overgrowth and overtopping of other corals (Fig. 3c, d, e), even those individually dominant in direct aggression (Fig. 3f; Maragos, 1972; Connell, 1973; Shinn, 1976; Tunnicliffe, 1980). Development of coral thickets also provides habitats for a remarkable array of reef fishes, invertebrates, and algae (Talbot, 1965; Glynn, 1973; Grassle, 1973; Patton, 1976; Ogden and Ehrlich, 1977; Brock et al., 1979) although the diversity of primary space occupiers is reduced (Talbot, 1965). Since corals capable of forming thickets or monospecific stands tend to have high growth rates (e.g. Randall, 1973a), their domination of a reef or reef zone may result in very high rates of reef development. The highest rates of reef growth so far reported are for reefs dominated by *Acropora cervicornis* (Macintyre et al., 1977), *A. palmata* (Adey, 1975; Macintyre and

* Reef extension: *Acropora* spp. (Mergner, 1971), *Montastrea annularis* (Jones, 1977), *Pocillopora damicornis* (Glynn et al., 1972; Glynn and Macintyre, 1977; Glynn, in press; Wellington, 1981), *Porites lutea* (Highsmith, 1980a), *Goniopora stokesi* (Sheppard, 1981). Initiation of patch reef formation: *Acropora cervicornis* (Gilmore and Hall, 1976; Shinn, 1976), *M. annularis* (Smith and Tyler, 1975), *Porites compressa* (Maragos, 1972), *P. lutea* (Highsmith, 1980a), Fungiidae (Sheppard, 1981). Development of thickets: *A. acuminata* (Randall, 1973a), *A. aspera* (Randall, 1973a), *A. attenuata* (Sheppard, 1981), *A. cervicornis* (Gilmore and Hall, 1976; Shinn, 1976), *A. formosa* (Davies et al., 1971; Sheppard, 1981), *A. hyacinthus* (Sheppard, 1981), *A. palmata* (Goreau, 1959; Scatterday, 1974), *A. spp.* (Pichon, 1971; Rosen, 1971), *Madracis mirabilis* (Bonem and Stanley, 1977; Bak and Engel, 1979), *Pocillopora damicornis* (Glynn et al., 1972; Glynn and Macintyre, 1977), *Porites compressa* (Maragos, 1972), and the ahermatypic coral *Lophelia pertusa* (Wilson, 1979). Avoidance of competitors and predators (Sheppard, 1979; Highsmith, 1980a).

Glynn, 1976), and *Pocillopora damicornis* (Glynn and Macintyre, 1977).

Further, fragmentation may play an important role in the rate at which coral reefs recover from hurricanes, which are exceedingly common over geologic time (see footnote, p. 210), or other disturbances. In some cases, reefs recover surprisingly fast, regaining their approximate pre-storm condition within 5 to 10 yr or less (Endean, 1973; Shinn, 1976). In other cases, where coral mortality was extremely high, recovery appears to require 2 decades or more. In 1961, for example, Hurricane Hattie destroyed 75-80 % of the corals, including 100 % of *Acropora cervicornis*, 80 % of *A. palmata*, and 50 % of *Montastrea annularis* on a 50-60 km wide section of the Belize barrier reef (Stoddart, 1974). Four years after the storm, the only significant frame-building corals present were those which survived the storm*. By 1972, some recruitment of *A. palmata* had occurred but *A. cervicornis* was still relatively uncommon. Areas farther from the center of the storm path had completely recovered by this time. Similarly, recovery of coral communities decimated by lava flows in Hawaii appears to require 20 to 50 yr (Grigg and Maragos, 1974) and recovery of reefs at Guam where over 95 % of the corals were killed by *Acanthaster*, may require 20 to 30 yr or longer (Randall, 1973b). Rapid recovery rates from storm damage have been attributed to the survival of coral fragments (Shinn, 1976; Highsmith et al., 1980). Slow recovery evidently occurs when a disturbance is so severe that hardly any fragments of the major reef-building corals survive. Thus, it appears that reefs recover rapidly when asexual reproduction and regeneration are possible but slowly when recovery depends upon sexual reproduction, probably reflecting high mortality rates for larvae and juveniles and possibly the low priority of sexual reproduction in the energy budgets of many corals (Table 8).

Survival of coral fragments may also facilitate recovery of reefs from dredging activities. On a dredged coral knoll at Diego Garcia, Sheppard (1980b) found many fragments and detached corals had survived. Subsequent growth of the corals frequently resulted in

reattachment, contributing significantly to consolidation of the dredge-produced talus (Sheppard, 1980b).

Finally, if asexual reproduction by fragmentation is as extensive as indicated by the data presented above, then there must be considerably fewer genotypes (evolutionary individuals of Janzen, 1977) than actual colonies on coral reefs. There is no information available in the coral literature on this point but there have been several studies on plants that form extensive clones vegetatively. Populations of grasses (Harberd, 1962, 1967) and aspens (Kemperman and Barnes, 1976) tend to have very few genotypes, to dominate large areas, and to attain very great age, in agreement with predictions presented earlier for corals and suggesting that the predictions may be applicable to primary-space occupying organisms in general.

CONCLUSIONS

Fragments, because of their relatively large size, are not subject to the high mortality rates of larvae and juveniles. In addition to local distribution, including acquisition of space from other species and colonization of new habitats, a coral can theoretically achieve virtual immortality by spreading the risk of death over many long-lived individuals capable of subsequently producing fragments also. Sexual reproduction in these corals, which may be restricted to release of gametes during short periods, results in broader dispersal than would be possible with fragments, thus serving as a hedge against the entire clone being killed during large-scale disturbances such as hurricanes.

The evidence presently available suggests that fragmentation may be the predominant mode of reproduction for many of the major reef-building corals, i.e. those most important ecologically in terms of abundance, energy flow, competitive ability, and creation of habitat for other organisms, and geologically in terms of primary reef-frame construction, rate of reef growth, reef morphology, and recovery from disturbances.

* Recruitment had occurred among corals that Stoddart (1974) did not consider significant frame-builders: *Agaricia*, *Millepora*, *Porites astreoides*, *Manicina areolata*, *Eusmilia fastigiata*, and *Mycetophyllia lamarckiana*. I predict that life histories of these corals will be most similar to those of the species in the upper portion of Table 8. *A. agaricites* is already listed and it is known that *M. areolata* has determinate growth resulting in small adult size (Goreau and Goreau, 1960). *P. astreoides* was the second most abundant species of juvenile coral at Bonaire and the third most abundant at Curacao (Bak and Engel, 1979) and does not attain large size (MacGeachy, 1977). Juveniles of *Millepora* and *E. fastigiata* were also relatively abundant at Curacao (Bak and Engel, 1979).

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Erratum

Re: Highsmith, *Mar. Ecol. Prog. Ser.* 7: 207–226, 1982

- Replace Table 6 on p. 215 as follows:

Table 6. *Porites furcata*. Substrate attachment relative to position within or adjacent to dense patches of the coral. Clump: colony located within the patch surrounded by other *P. furcata*. edge: edge of patch; hole: hole within or adjacent to the patch (see Fig. 2d); other: corals of other species or coral debris; attached: connected to substratum, detached: not connected to substratum; loose: stem broken but supported in growth position by neighboring colonies. Values expected by χ^2 test are shown in parentheses.

Location	Position	Attached	Detached	Loose	Dead	Other	Total
Achutupo	Clump	151 (116)	8 (138)	437 (250)	20	7	623
	Edge	18 (22)	52 (26)	42 (64)	25	11	148
	Hole	8 (39)	150 (46)	42 (115)	295	324	819
	Other			1		47	48
	Clump	166 (129)	5 (157)	529 (413)	27	10	737
Bugatupo	Edge	4 (19)	49 (23)	49 (60)	7	11	120
	Hole	19 (41)	176 (50)	26 (130)	202	290	713
	Other					68	68
	Clump	165 (133)	9 (107)	371 (292)	20	14	579
Salar	Edge	12 (22)	38 (20)	40 (48)	1	13	104
	Hole	23 (45)	133 (40)	28 (99)	68	525	777
	Other	1		1		176	178
	Total	567	620	1566	665	1496	4914